

BRIAN BLUNDELL BOYCOTT  
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*B.B. Boycott*

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Brian Blundell Boycott was an outstanding zoologist and neurobiologist. His early research (1947–52), at the Anatomy Department of University College London and at the Stazione Zoologica in Naples, Italy, was on learning and memory in cephalopods and the functional architecture of the octopus brain. From 1952 to 1970 he was a teacher of zoology and later neurobiology at University College London (Zoology Department). Brian's research interests changed in the early 1960s, when he began studying the mammalian retina. Over a period of 35 years he produced many seminal papers that laid the foundation for our modern understanding of the cell types and synaptic connections that form the basis of parallel processing in the retina. In 1970 Brian moved to the Medical Research Council (MRC) Biophysics Unit at King's College London, from which he retired as Director at the end of 1989. He continued to be an active researcher at Guy's Hospital Medical School (1990–97) and in the Institute of Ophthalmology, University College London (1997–2000). Brian was a modest and kind person, generous in sharing ideas and material; he liked to interact and cooperate with other people and was very supportive of young scientists.

### ANCESTRY, FAMILY AND SCHOOLING, 1924–42

When Brian's colleagues and former students celebrated his 65th birthday by holding a scientific symposium in June 1990 at Leverett House, Harvard University (Dowling *et al.* 1991), signs were put up in the college announcing the 'Boycott Festschrift'. Very much to the amusement of Brian, a group of students standing in front of the signs asked themselves: 'why should we boycott fresh fish?' However, I have to confess that, until recently, I was equally ignorant of the origin of the word 'boycott', just as those students did not know the word

'Festschrift' taken from the German academic tradition. In his memoir (41)\* Brian explains that 'boycott' is a rather recent addition to English, French and German. C.C. Boycott (1832–97) was a farmer and an agent for Lord Erne in County Mayo, Ireland. Landlords and their agents were not popular and the Irish Land League, in opposition to foreign domination, used the tactics of social and economic blockade. By chance the long blockade of C.C. Boycott in his home during 1880 became world famous: an American journalist, James Redpath, was the first to describe these blockades as a 'boycott'.

Very little is known about Brian's ancestry, so his roots cannot be traced. Brian was an only and rather solitary child. When he was seven years old, his mother separated from his father, taking Brian with her. This must have happened after a long period of difficult family life. His father later lost his job as manager of an insurance company and provided no support for his wife and son. Brian's mother was fortunate to get a job as a sales assistant at the firm where she had been apprenticed before her marriage. However, in 1932 unemployment was high and pay was low, so Brian's mother could afford to rent only a single room. Under such difficult circumstances it was Brian's salvation that he was admitted to a charity school sponsored by the Freemasons. In addition to tuition and schoolbooks, Brian was provided with clothing and food during semesters.

Brian was regarded as a sickly child and had many childhood ailments: measles, whooping-cough, double lobar pneumonia and acute bilateral mastoiditis in 1935. The sum of illness and family disruption during Brian's early years left their mark and it is therefore hardly surprising that he performed badly in school and was always at the bottom of the class.

Brian's health improved from 1936 onwards. He moved to the senior school, and new subjects such as history, English literature, biology, physics and chemistry attracted his attention. He spent much of his spare time either reading biology books or observing pondwater with a microscope and collecting animals and plants in the surrounding countryside. However, he failed French and mathematics, and just managed to pass physics and chemistry.

#### BIRKBECK COLLEGE AND NATIONAL INSTITUTE FOR MEDICAL RESEARCH, 1942–46

Brian's poor school record and financial situation prevented him from enrolling at a traditional British university. Once again he had to do things the hard way. Birkbeck College, founded in 1823 as the London Mechanics' Institution, was incorporated into the University of London in 1920, with the proviso that it should teach only evening and part-time students. Brian registered to read honours zoology with subsidiary botany in September 1942. Just before he joined Birkbeck, most of the Zoology Department had been bombed during the Blitz, and the classes had to be held in the remains of the building. Later, because of the night-time air raids, teaching was changed from weekday evenings to daytime on Saturdays and Sundays. The principal zoology teachers were Alastair Graham (F.R.S. 1979) and Vera Fretter, whom Brian characterized as 'outstandingly good, enthusiastic, and helpful to students with academic and other problems' (41). With the help of great teaching, Brian gained his science degree in 1946 with first-class honours in zoology.

Brian had to find a job while studying part-time at Birbeck College. After several attempts

\* Numbers in this form refer to the bibliography at the end of the text.

at various places, he finally got a job as an animal-house attendant at the National Institute for Medical Research (NIMR) in Hampstead. He learnt animal care the hard way and, more importantly, he was exposed to people with no academic ambition or background, to people who had sets of values and motivations different from those he had experienced. In retrospect this experience left its traces on his character. Brian socialized easily with people from greatly different backgrounds. Forty years later, at the Max Planck Institute in Tübingen, he became a good friend of Herr Baur, one of the people who worked in the animal house. Herr Baur owned a small farm with a vineyard and produced his own bread, delicious sausages, excellent wine and apricot brandy. Every so often Brian pretended that he was not hungry when the members of the laboratory went for lunch. Instead he secretly enjoyed a frugal lunch with Herr Baur in the animal house. On the other side of the coin, Brian could not tolerate academic snobbishness and elitist behaviour.

Brian worked in the NIMR animal house for a few months before he was moved to the physiology laboratory as a general dogsbody and washer-up. This laboratory was something special because it was formerly that of Sir Henry Dale, F.R.S.—and even 50 years later Brian reported this with the greatest respect. Dale, who was one of the most distinguished pharmacologists of the twentieth century, discovered chemical synaptic transmission; his work was honoured with the Nobel Prize in 1936, jointly with Otto Loewi (For.Mem.R.S. 1944) (Feldberg 1977). Dale had retired the year before Brian joined the NIMR, but his authority and analytical style permeated the place. The technicians were under the iron discipline of Dale's former assistant, L.W. Collison. These were the days when apparatus had to be designed and made in-house for a particular experiment and Brian acquired a lot of practical skills. Later in life he always carried a 'Swiss Army officer's knife' in his pocket; not the simple version but the elaborate one that serves many different purposes: it can be used as a knife, as a screw-driver, as a saw and, most importantly, as a bottle opener.

While Brian was at the NIMR, the laboratory worked on physiological problems of personnel involved in naval warfare, under the direction of G.L. (later Sir George) Brown (F.R.S. 1946). One experiment involving Brian was concerned with a search for drugs to ameliorate seasickness among troops making amphibious landings. Another experiment concentrated on problems of diving physiology, particularly the effects of oxygen at high pressure and carbon dioxide narcosis. Apparently Brian was more useful than just a washer-up because, when he received his armed services call-up paper, Brown had a reservation order slapped on him.

During his time at Birkbeck College, Brian met Marjorie Burchell, who also studied biology and worked at the NIMR and later became his wife. Despite the problems of balancing part-time study with full-time work during the war years, they managed on Saturday nights to go to the theatre to see many of the now legendary productions of the Old Vic company. Marjorie and Brian were happily married for nearly 50 years. Marjorie loyally supported Brian and provided a secure family base from which he could dedicate his life to science. She and Antony, their son, were a wonderfully supportive and tolerant family. Brian and Marjorie, both trained in biology, kept a vivid interest in animals and plants throughout their marriage. Walking with them through the greenhouses of Kew Gardens in London was always a delightful and stimulating botanical excursion. It is gratifying that, just a few years ago, they could visit Australia together and finally see what Brian considered to be the most beautiful natural scenery.

UNIVERSITY COLLEGE LONDON AND STAZIONE ZOOLOGICA, NAPLES,  
1946–52

In 1946 Brian was appointed to an assistant lectureship in Zoology at University College London (UCL). His main task was to teach the practical part of the course, and he also registered to do a PhD at the same time. Shortly afterwards, J.Z. Young, F.R.S., who was Professor of Anatomy at UCL, advertised for a research assistant to work both in London and at the Stazione Zoologica in Naples, Italy, on the brains and memory mechanisms of cephalopods (Young 1996) (38). Brian applied for the position, supported by the Nuffield Foundation, and was appointed against long odds. He writes, 'For a zoologist applying for Young's research assistantship, the romance and prestige of the Naples laboratory was as attractive as his very high and dynamic reputation' (38). The Stazione Zoologica was founded in 1872 by Anton Dohrn, using his private fortune (Florey 1985; Heuss 1991). Dohrn's very idealistic motive for the foundation was his conception of biological research as a free international cooperation of individual scientists. The Stazione Zoologica was the first marine biological laboratory, enormously successful and internationally admired. It became a centre at which many of the leading biologists of Europe and some from the USA worked at one time or another during their careers. To give just one example, in 1966 Bernard (later Sir Bernard) Katz, F.R.S., and Ricardo Miledi (F.R.S. 1970) from UCL came to the Stazione Zoologica to investigate the relationship between  $\text{Ca}^{2+}$  ions and transmitter release. Their experiments have become classics: they showed that calcium entry into the presynaptic terminal of the axo-axonic synapse in the stellate ganglion of the squid is essential for transmitter release (Katz & Miledi 1967).

Brian's work in Naples concentrated on the learning mechanisms in the octopus. The following three major approaches were taken.

*Anatomical studies of the central nervous system of the octopus*

Young and Boycott largely used reduced-silver staining methods to study the fibre tracts, and applied lesion and degeneration methods to reveal the connections between the different lobes of the octopus brain. Reduced-silver or neurofibrillar methods stain parts of the cytoskeleton of nerve cells, the neurofilaments. The axons of most nerve cells and the dendrites of some nerve cells show up in reduced-silver stained preparations. In addition, Young and Boycott used the Golgi method to stain individual neurons, sometimes quite successfully. The Golgi method is a silver impregnation, very selective and erratic, often regarded as the 'prima donna' of neuroanatomical methods. Although the Golgi method stains only a few nerve cells at random, they are often completely stained, including their dendrites and axons. Both the Golgi method and the reduced-silver method were brought to perfection by the Spanish neuro-anatomist Santiago Ramón y Cajal, who was Brian's greatest scientific hero by far. The work went well and a first draft of a large book, *The anatomy of the brain of Octopus vulgaris*, was finished in 1952. However, Young continued to work on it for another 20 years (Young 1971) and Brian's role in this study is described in his generous preface to the book.

*Learning in the octopus*

These investigations were pursued in Naples rather than Britain because the chosen experimental animal is found in considerable numbers along the shores of the Mediterranean. Brian wrote (8):

The octopus is cooperative; if it is provided with a shelter of bricks at one end of a tank of running seawater, it takes up residence in the shelter. When a crab or some other food object is placed at the other end of the tank, the octopus swims or walks the length of the tank, catches the prey with its arms and carries it home to be poisoned and eaten. Since it responds so consistently to the presence of prey, the animal is readily trained. It is also tolerant of surgery and survives the removal of the greater part of its brain. This makes the octopus an ideal animal with which to test directly the relation between the various parts of the brain and the various kinds of perception and learning.

After several false starts (1), Brian devised a very successful training regime: a crab was put in the tank together with some kind of geometric figure—say a square—and the octopus was given an electric shock when it made the normal attacking response. With this simple method Brian found that octopuses could learn not to attack the crab when a square was shown, but to go on attacking a crab shown without one. This simple learning model, to be rewarded for one sort of stimulus and shocked for another, became the basis for many subsequent experiments (Young 1964).

#### *Electrical stimulation and surgical ablation of the brains*

The electrical stimulation experiments were first performed on restrained lightly anaesthetized animals. On the basis of evoked responses, Brian functionally classified the lobes of the octopus brain into a hierarchical scheme, with lower motor centres, higher motor centres and association areas. However, the major aim was a study of the neural control of behaviour, and this required electrical stimulation of the brain of unrestrained animals. Initial experiments were promising, and discrete patterns of behaviour could be evoked (6). However, the experiments finally failed because of electrode instability problems. Much more successful were the studies on how the surgical ablation of parts of the brain affected octopus learning. An octopus with the vertical and/or superior frontal lobes removed could not remember that an attack on a crab presented with a square resulted in a painful electrical stimulus. In a series of elegant experiments, Brian was able to show that the long-term memory, as it is now known, was abolished if the lobes were removed, while the short-term memory remained intact (2, 3). Eliot Stellar pointed out (Stellar 1957) the parallels between these results with invertebrates and the unexpected discovery of a similar effect after the bilateral removal of the hippocampus in man by W.G. Penfield, F.R.S., B.A. Milner (F.R.S. 1979) and W.B. Scoville (Milner 1998; Milner *et al.* 1998).

The octopus experiments performed by Brian in Naples were extremely successful and laid the ground for future experiments by Stuart Sutherland on form perception (Sutherland 1968) and by Martin Wells on tactile discrimination (Wells 1978). Although J.Z. Young supported Brian's plans that some of the octopus studies be written up as Brian's PhD thesis, Young insisted that writing this or that paper had higher priority. Brian therefore never had time to obtain a PhD, although the results he produced between 1947 and 1952 on the octopus brain are far beyond the demands of any PhD thesis. Later in life, Brian never admitted that this might be a loss, but rather was proud that he was made Professor without having obtained a PhD. Nevertheless, Brian was very pleased when Britain's Open University awarded him an Honorary Doctorate in 1988.

Brian not only became an independent scientist during his working periods at the Stazione Zoologica in Naples. His first exposure to a foreign country and the lifestyle of the Neapolitans made a deep impression on him. Brian's stories about life in postwar Naples were not only entertaining, they were also good lessons on human behaviour under difficult circumstances. The truly international intellectual atmosphere and the stimulating interactions with

other scientists at the Stazione Zoologica left their imprint on Brian. The head of the Stazione, Reinhard Dohrn (1880–1962), of German origin, raised in Italy and married to a Russian, was a true European (Götze 1964; Boverly 1982; Groeben 1983). The Dohrns incorporated Brian into a family atmosphere that he had not experienced in his earlier years. Reinhard Dohrn was a man of broad culture, and it was his influence and standards that slowly changed Brian during the years he spent in Naples. From a parochial English boy Brian became an ardent European, and he very much disliked British isolationism.

#### UNIVERSITY COLLEGE LONDON, ZOOLOGY DEPARTMENT, 1952–70

During these years teaching took an increasing portion of Brian's time, and the direction of his research changed from the octopus brain to the vertebrate brain and finally to the mammalian retina. In his autobiography (41), Brian gives a detailed account of the teaching situation and its changes from 1952 until 1970, which can only be summarized briefly here. The basic design of the zoology honours course at UCL was about 50 years old, with the exception of comparative physiology, which had been introduced in the mid 1930s. Together with David Blest (now in Canberra, Australia), Brian ran a new neurobiology course that became popular and successful. By the 1960s, the old honours system was too inflexible to incorporate modern science, and the university courses were restructured to bring in a modular system resembling the scheme long established in American universities. Good, mandatory, basic general courses were the backbone of this new scheme. Brian was in charge of, and taught most of, a basic zoology course lasting three terms. However, because of rivalries between the departments it could not be a biology course but was an interdisciplinary course for students majoring in psychology, chemistry, biochemistry and anthropology. In addition to this basic zoology course, Brian was also involved with an interdepartmental course in basic neurobiology. The head of the zoology department, M. Abercrombie, F.R.S., was very supportive but when he left in 1968 to become Director of the Strangeways Laboratory in Cambridge, the search for his successor was difficult and Brian became the interim head. He wanted to set up a high-powered teaching committee to plan and fund basic biology courses. However, Brian did not receive the necessary support from the Provost of UCL and he resigned. He accepted the long-standing persuasions of King's College London, to join the MRC Biophysics Unit there. For the rest of his life Brian was sorry that he had resigned from UCL because he was happy to combine teaching and research, and he was deeply convinced that this was the duty of university academics. He felt that the decline of this tradition was bad for the students but even more so for the researchers. Brian was very pleased when in 1980 he became a member of the Swinnerton-Dyer Committee on Academic Organization of the University of London. He could infuse into the proposals made by this committee some of his ideas about how university teaching should be reformed.

Brian continued his cephalopod work until 1965 (8, 9). He realized that, to relate the behavioural responses to different parts of the brain, it would be necessary to perform electrical recordings from these areas. Recording the electrical activity was also important because a theory for memory storage, formulated by the physiologist Alexander Forbes (Forbes 1922), suggested that memory was sustained by dynamic reverberating activity within a closed interconnected loop of self-exciting neurons. This theory was favoured by Young (1964). However, despite many attempts Brian failed to record the activity of single neurons in the octopus brain.



The reason seems to be that when electrodes are inserted into the brain, the mechanical disturbance evokes vasomotor reflexes that locally shut down the blood supply. Presumably this is because cephalopod blood does not clot; the result is death of the nerve cells at the electrode (31). It was wise that Brian finally gave up research on the cephalopod brain because another marine animal, *Aplysia*, also from the shore of the Mediterranean, turned out to be more 'cooperative' than the cephalopods. This animal shows simple forms of learning such as habituation, sensitization and classical conditioning. Behavioural, electrophysiological and molecular genetic studies in *Aplysia* were honoured by the award to E.R. Kandel of the Nobel Prize for Physiology or Medicine in 2000 (Kandel & Squire 2000). Although cephalopods in retrospect were not the ideal model for learning and memory, they turned out to be the animal of choice for another study. Their giant axon, discovered by Young (1936), became the ideal model system for studying the biophysics of nerve conduction. The seminal studies of the ionic basis of the action potential performed by A.L. (later Sir Alan) Hodgkin, F.R.S., and A.F. (later Sir Andrew) Huxley (P.R.S. 1980–85) on the giant axon were honoured with the Nobel Prize for Physiology or Medicine in 1963 (Hodgkin 1977).

In about 1958 Brian's interests in learning and memory formation gradually shifted towards the hippocampus in reptiles and other vertebrates. This was triggered by the apparent similarity between the effects of lesions of the vertical lobes of the octopus brain and the defects observed in the famous patient 'H.M.', who suffered from bilateral damage of the hippocampus (for a review see Milner (1998)). Together with R.W. Guillery (F.R.S. 1983), Brian studied the fibre connections in the reptilian hippocampus by looking at axonal degeneration after lesions. Because rates of degeneration were known to vary with body temperature, the animals were kept at different temperatures. Guillery and Boycott came across an unexpected phenomenon: they observed in their preparations numerous small neurofibrillar rings, which seemed to be synapses (4, 5, 7). Moreover, the frequency of the rings varied between animals kept at lower (20 °C) and at higher (30 °C) temperatures. Because synaptic changes, according to the famous model (Hebb 1949) proposed by Donald Hebb (F.R.S. 1966), represent the structural correlate of learning, these findings in reptiles by Guillery and Boycott offered the exciting prospect of producing synaptic changes simply by varying environmental conditions. Together with E.G. Gray (F.R.S. 1976), the pioneer of studying synaptic structure by electron microscopy (Guillery 2000), they showed that the neurofibrillar rings are a torus of neurofilaments in the presynaptic terminal (7). However, because such ring-like structures are not seen in the cerebral cortex, which is densely populated with synapses, they could not be used as a 'marker' to study synapses by light microscopy (Guillery 1998).

The subject of neurofibrils, which are bundles of neurofilaments, fascinated Brian for the rest of his life. Much later, in the MRC Biophysics Unit, neurofilaments became a major theme of the group. And even later, in cooperation with Leo Peichl, Brian perfected methods for the neurofibrillar staining of retinal whole mounts to study horizontal cells and alpha ganglion cells. Nowadays, when immunocytochemical methods have made selective staining so precise, one cannot imagine that Brian had to toil for hours to find the right composition of water (the 'Agua gorda' of Ramón y Cajal) that would give optimal results with the reduced-silver or Golgi methods. Ramón y Cajal (Cajal 1989) has described the reward of such passion as follows:

Hence, when chance permits an investigator to create a new selective staining method or to perfect in a fortunate way one already known, histology sensibly extends its horizon. The harvesting of new and significant facts, the cataloguing of forms and structures, is performed easily and refreshingly as if one reaped at will in a wheat-field sown by others.

In the early 1960s Brian was convinced that synaptic changes represent the memory traces in the brain. Because the neurofibrillar rings did not prove to be a reliable marker of synapses, Brian focused on dendritic spines, which had been shown by electron microscopy to be post-synaptic structures (Gray 1959). He was also familiar with an old observation by Querton (1898) that hibernating alpine marmots have fewer spines on cerebral cortical pyramidal cells than awake animals. Brian thought it would be important to repeat that study; however, it was not possible to do this in alpine marmots. At the right moment, in 1963, Brian was invited by John Welsh to visit Harvard and teach his invertebrate zoology course while Welsh was on sabbatical leave. Hibernating mammals are more readily available in North America than in Europe and, in particular, ground squirrels are abundant. During Brian's stay at Harvard, the Golgi staining of ground-squirrel cerebral cortex worked well. However, it was impossible to find sufficient numbers of exactly comparable pyramidal cells in the two ground-squirrel populations (hibernating and awake). Nevertheless, Brian could readily observe differences in the Purkinje cells of the cerebellar cortex, which made a second visit to the USA worthwhile.

Brian returned to Welsh's laboratory to continue his studies of dendritic spines, and here it was that chance entered his research programme. He shared the animals provided by Charles Lyman of the Harvard Medical School with John E. Dowling, who studied the structure of the vertebrate retina by electron microscopy. Dowling had obtained some electron micrographs of presumed synapses in the ground-squirrel retina, but hardly anything was known of the neuronal cell types in that retina. Brian had observed changes in the dendritic spines of Purkinje cells between hibernating and awake animals, but details of the changes could not be resolved by light microscopy. They decided to collaborate; Dowling began to study Purkinje cell spines by electron microscopy, and Brian studied ground-squirrel retinæ with the Golgi method. Both projects yielded interesting results, but the retinal project turned out to be the winner. Brian became more interested in the retina, 'an approachable part of the brain' as Dowling put it later (Dowling 1987), and they decided to cooperate. What happened by chance became a merger of interests and talent. In the summer of 1964, Brian joined Dowling in Baltimore at the Wilmer Institute, where Dowling had recently moved. That started a decade of extended trips by Brian to the USA, and a close collaboration with Dowling.

They first continued work in Baltimore on the ground-squirrel retina, but the breakthrough came when they turned to the primate retina, in which they were able to identify the bipolar and amacrine cell synapses in the inner plexiform layer as well as the photoreceptor synapses in the outer plexiform layer. Their first report was at the Cold Spring Harbor Symposium in 1965, followed by their paper in the *Proceedings of The Royal Society*, series B, in 1966 (10, 11). In this paper they published a wiring diagram of the mammalian retina that became so popular that even now it is reproduced in nearly every textbook of anatomy, physiology or neurobiology as the classical retinal scheme. The paper itself became a citation classic. The electron microscopical results made it clear that some reassessment of the light microscopy of the primate retina was needed. Brian succeeded in producing superb Golgi-stained sections of the primate retina. They are now kept in the Max Planck Institute in Frankfurt, and it is still a pleasure to observe the beauty of the stained cells. On the basis of this material Brian and Dowling published their *Philosophical Transactions* paper on the organization of the primate retina (12). Brian also cooperated with other people in Dowling's laboratory, particularly with Helga Kolb and Steve Fisher. In 1965 William K. Stell had succeeded in studying Golgi-impregnated cells of the fish retina by electron microscopy (Stell 1965). Kolb applied this technique to the primate retina and, together with Brian and Dowling, they described two

types of midget bipolar cells contacting the cone pedicles: flat and invaginating midget bipolar cells (13). Kolb and Brian worked together for four years during his annual visits to Dowling's laboratory; later, when Kolb moved to the National Eye Institute in Bethesda, they continued a fruitful cooperation for several more years. After studying the cone contacts of monkey and cat bipolar cells, Kolb and Brian elucidated the connectivity of horizontal cells of the primate retina, and they began to generalize these results to other mammalian retinæ, particularly the cat retina (14, 15). With Fisher, Brian studied the synaptic connections made by horizontal cells in the cat and the rabbit retina (16). They were surprised that these cells formed hardly any chemical synapses. Even now, more than 25 years later, it is a matter of debate whether horizontal cells act by a  $\text{Ca}^{2+}$ -independent non-synaptic release of the inhibitory transmitter  $\gamma$ -aminobutyric acid (Schwartz 1999), or whether they provide an electrical feedback signal to the photoreceptor terminals (Kamermans *et al.* 2001).

In 1975 Brian published his last paper in this extremely successful collaboration with Dowling's laboratory (18). In 1967 Alan Laties had observed, with the use of catecholamine-induced fluorescence, an unusual type of retinal neuron branching both in the outer and inner plexiform layers, now called an interplexiform cell. Brian first disputed the existence of such neurons, which neither he nor Ramón y Cajal had seen before. However, over several years he collected many Golgi-stained retinæ in which he could observe these cells and finally convinced himself that they were real. Over these years Dowling, Kolb, Fisher and Stephen Yazulla defined the synaptic connections of these cells. Alan Laties has described the final part of the interplexiform cell study as follows:

The manuscript was largely written by Brian who took great care to be sure that every fact was nailed down and that every statement made had been amply confirmed. Thereafter, I shared with my co-authors the satisfaction common to all researchers at the publication of the manuscript; however, satisfaction was tinged with wistfulness in the knowledge that a wonderful collaboration had come to an end.

#### MRC BIOPHYSICS RESEARCH UNIT AT KING'S COLLEGE LONDON, 1970–89

The first Director of the MRC Biophysics Unit at King's College was J.T. (later Sir John) Randall, F.R.S. It was in this unit that M.H.F. Wilkins (F.R.S. 1959) and R. Franklin were able to provide the crucial X-ray diffraction data for J.D. Watson (For.Mem.R.S. 1981) and F.H.C. Crick (F.R.S. 1959) to construct their double-helix model for DNA (Crick 1974; Klug 1974). On the basis of these early successes, the MRC Unit and the Department of Biophysics moved into their own building in Drury Lane. Wilkins succeeded Randall and wanted to move the unit towards neurobiology; he therefore appointed Brian. The MRC split the Biophysics Research Unit into a muscle group headed by Jean Hanson (F.R.S. 1967) and a neurobiology group headed by Brian. The attraction of King's for Brian was the presence of cell biologists and the chance to tackle fundamental problems of neurobiology such as the growth and differentiation of nerve cells, along with the question close to his heart as a morphologist: what determines the shape of a nerve cell? It was not Brian's aim to build a department in which he would instruct the scientists to pursue his own research interests. Instead, he created small independent groups that planned and executed their own projects.

The first appointment that Brian made was David Gilbert, who had discovered how to extract the axoplasm from the giant axon of the fan-worm *Myxicola infundibulum* as an intact

protein gel. It turned out to be composed almost solely of neurofilaments (Gilbert 1975*a,b*), and his work on neurofilaments formed a wonderful bridge between Brian's earlier interests in neurofibrils and the strong molecular structural expertise of the old Biophysics Unit. This work was tragically cut short by David's premature death in 1980 (22).

Brian also appointed John Scholes, the only 'retinal person' in the neurobiology group; Scholes had traced the synaptic wiring of the different colour cones in the fish retina (Scholes 1975) and found it an ideal tissue for studying neural development because new nerve cells are continuously added at the periphery of the retina. Scholes is now at the Department of Anatomy and Developmental Biology, University College London. His research interests are the development of the visual system and the behaviour of microglia in the central nervous system.

Dennis Bray was recruited from the MRC Laboratory of Molecular Biology in Cambridge, and conducted his classic studies of growth cone motility (Bray 1979) and organelle movement in axons while a member of the King's group at Drury Lane. He is now a member of the Zoology Department at Cambridge University and the aim of his present work is to understand how small biochemical 'circuits', composed of receptors, kinases and other proteins, relay messages within and between cells.

When M.H.F. Wilkins retired as Director in 1980, there was a long and stressful period of uncertainty about the future of the unit. It ended with the surprising offer by the MRC to Brian, to direct the unit as a cell biophysics institute together with D.A. (later Sir Dai) Rees (F.R.S. 1981). Rees, known for his studies of carbohydrate structure, retained his position with Unilever and worked part-time at King's. Brian and Dai Rees appointed R.M. Simmons (F.R.S. 1995) and J. Sleep to strengthen the muscle group, and G. Dunn to study fibroblast locomotion.

The last of Brian's appointments to the unit was Jeremy Brockes (F.R.S. 1994), who studied the neural control of amphibian limb regeneration. He is now an MRC Research Professor in the Department of Biochemistry and Molecular Biology at University College London, where he continues to work on limb regeneration and recently began to study the cell biology of prion diseases.

Although these people worked completely independently on different projects, there was an excellent exchange of ideas and methods. The diversity of the work reflected Brian's wide interests, and he took great pride in being able to support such a wide range of successful scientific projects not directly related to his own research.

Rees soon left King's to become Director of the National Institute for Medical Research and, later, Executive Secretary of the MRC. In 1989 Brian retired as Director. The unit's work had been favourably reviewed and it was restructured as the MRC Muscle and Cell Motility Unit, directed by R.M. Simmons. This shared the Drury Lane building, now named the Randall Institute, with a new Developmental Biology Research Centre. The seeds thus sown have bloomed, and in 1998 the Randall Institute moved to new accommodation at New Hunt's House, in the King's College Guy's Hospital campus at London Bridge, leading to the formation of the Randall Centre.

## PERSONAL RESEARCH FROM 1974 TO 2000: A EUROPEAN COOPERATION

After the International Physiological Congress in Munich in 1971, there was a Satellite Symposium to which O.D. Creutzfeldt, my PhD supervisor, had invited leading scientists in hearing and vision research; among them was Brian. My interests at that time were concentrated on spatial resolution in the cat visual system, so I asked Herr Professor Boycott 'What are the smallest ganglion cells in the cat retina?'. He answered, 'Oh boy, what a silly question...' but invited me to come to London and look down the microscope to find out for myself. In spring 1972 I went to Brian's laboratory in Drury Lane and saw for the first time his beautiful Golgi-stained whole mounts. From that moment, I was converted from a physicist into a neuroanatomist. In only six weeks we performed a morphological classification of the ganglion cells of the cat retina (17). This work, together with the X/Y classification of Enroth-Cugell and Robson (1966) and the physiological studies of the Australian groups (Levick 1996), laid the groundwork for the concept of parallel processing in the mammalian retina, by which the image projected onto the retina is sampled in parallel by distinct functional types of ganglion cells, which transfer separate messages to the visual centres in the brain.

This European cooperation lasted for nearly 30 years. Brian visited Germany frequently: first when we worked together at the Max Planck Institute in Munich, later at the University of Konstanz, at the Max Planck Institute in Tübingen, and for the last 18 years at the Max Planck Institute for Brain Research in Frankfurt. His visits were always periods of intensive work, and the heated discussions about cell types became legendary in the laboratory. The working periods were interrupted by wonderful excursions to the countryside, to romantic old cities, to baroque churches and castles. Many evenings, exhausted from work, we ended up at the local pubs (Weinstube), drinking wine from the area and talking about everything except science. It was great fun to be with Brian; for example, in conversations he could elucidate the similarities and general principles of flying buttresses of Gothic churches, of the iron glass houses in botanical gardens and of the cytoskeleton of nerve cells.

After finishing the ganglion cell paper, and after a postdoctoral period of mine in Canberra with P.O. Bishop (F.R.S. 1977), B.G. Cleland and W.R. Levick (F.R.S. 1982), we joined forces again. Together with Leo Peichl, my PhD student, we started to work on the horizontal cells of the cat retina. Brian had stained horizontal cells by the Golgi method years before in collaboration with Helga Kolb. However, because the Golgi method depicts only isolated cells at random, a population analysis was not possible. We now found, in contrast, that the reduced-silver method stains all A-type horizontal cells including their dendritic trees, and thus the mosaic of their cell bodies and the way in which their dendritic fields tile the retina could be studied. The cell body array was shown to be regular and the dendritic tiling was found to be uniform. Using a 'nearest-neighbour analysis' we were able to show that the A-type and B-type horizontal cells each form statistically regular mosaics, and that A and B mosaics are arrayed independently. Thus, the regularity of a mosaic became an objective definition of a cell type. In future work we were reluctant to accept a new type of cell identified under the microscope if we were not able to map the retinal mosaic of such cells (40). Our study of cat horizontal cells was submitted as a series of three papers to the *Proceedings of The Royal Society*, series B (19–21). Brian had written one paper and I had written—in my Teutonic English—the other two papers. Although the reviews were quite favourable, one reviewer complained that the English style of the paper written by Brian was not quite appropriate—a fine example of British humour!

After Leo Peichl had finished his PhD he joined Brian as a postdoctoral worker and spent a year at King's. Brian and Leo perfected the reduced-silver staining of whole retinæ so that alpha ganglion cells in the cat retina could be consistently stained (24). Later this enabled Brian and Leo to examine a variety of species and to show that in most mammalian orders alpha cells comprise about 5% of the ganglion cell population (29, 30). Together with D.I. Vaney, at that time a postdoctoral worker in my laboratory, Brian and Leo identified cholinergic amacrine cells by neurofibrillar staining in the rabbit retina, and also described a population of long-range amacrine cells in that retina (26, 32). As a result of the consistent staining of alpha ganglion cells it became possible to study the mosaics of ON- and OFF-alpha cells separately (25). ON- and OFF-cells form independent arrays, and their dendritic fields show minimal overlap. This suggested to us that, during development, dendrites of identical nerve cells exhibit a territorial behaviour (27).

Brian also pursued his own research projects in London. There he was supported by John M. Hopkins, a very gifted and loyal technician he had 'inherited' from J.T. Randall. Over the years Hopkins became an expert in sectioning Golgi-stained cells for electron microscopy and thus was able to reconstruct their synaptic contacts. Together with Hopkins, Brian identified microglia cells of the primate retina that could easily be mistaken by light microscopy for horizontal cells (23). When H.G. Sperling from the University of Texas at Houston spent a sabbatical in London, he and Brian studied horizontal cells of the primate retina. Sperling had a long-lasting interest in primate colour vision, so they looked for a possible cone selectivity of primate horizontal cells and found none (28). This was the first anatomical evidence that the receptive field surround of ganglion cells of the primate retina receives input from both the red and the green cones.

After retiring from the directorship of the MRC Cell Biophysics Unit at King's, Brian joined the Department of Anatomy of Guy's Hospital Medical School (University of London) in 1990 as Professor Emeritus. He continued to be productive there and, together with Hopkins, he performed elaborate studies of the synapses made by bipolar cells at the cone pedicle of the monkey retina (35). In the new surroundings at Guy's Hospital, Brian made many friends, and the stimulating atmosphere there with many young enthusiastic scientists was a kind of elixir that kept him young. Everybody enjoyed discussing problems of neurobiology with Brian, and in addition he was a kind of father figure, giving advice about personal problems. When the Institute of Ophthalmology at the University of London offered him the opportunity to join the Institute as Professor Emeritus in 1997, he was very pleased and became an active member of this outstanding institution.

After Brian's retirement from King's we intensified our cooperation. In the meantime, in Frankfurt we had succeeded in staining horizontal cells of the primate retina with immunocytochemical methods. Together with Brian, who had beautiful Golgi preparations of primate horizontal cells, we studied their cone connectivity (33, 34). We were fascinated by the complexity of interactions at the first synapse of the retina, the so-called cone pedicle, and became interested in the different types of bipolar cell that received light signals from the cone pedicle. From Brian's Golgi-stained whole mounts we identified 10 different types of bipolar cell (36). We also succeeded in finding selective markers for these bipolar cells (Grünert *et al.* 1994), while Brian and Hopkins studied their cone contacts (37). During his frequent visits to Frankfurt Brian also met the young PhD students in my laboratory. At the beginning they were a bit shy. Being educated in the German academic system, they did not expect the famous old professor from England to be so easy-going. Brian was very skilful in breaking this barrier and

soon they not only discussed their scientific projects with him but also invited him to their parties. Thus he became involved in several projects with the younger people of my laboratory (S. Löhrike, J. Röhrenbeck and D. Sandmann), in projects they actually did for their PhD theses.

It is gratifying that Brian's numerous important contributions to retinal research were honoured in the spring of 1999 by the Association for Research in Vision and Ophthalmology (ARVO), which awarded the Proctor Medal to Brian and myself (39).

In December 1999, Brian was just recovering from a serious operation in London when I sent him an early draft of a paper. He returned the manuscript with many excellent suggestions for improvements and in the accompanying letter he wrote, 'I think you are generous to include my name. I won't argue because when it comes out in 2000 it will be the 50th anniversary of my first published paper. This appeals to me'. Unfortunately Brian did not live to see the publication of this paper (40) and passed away on 22 April 2000.

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The frontispiece portrait was received from Godfrey Argent in 1971, and is reproduced with permission.

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